

## A LATE TRIASSIC DROMATHERIID (SYNAPSIDA: CYNODONTIA) FROM INDIA

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## ABSTRACT

A dromatheriid non-mammalian cynodont, *Rewaconodon tikiensis*, gen. et sp. nov., is described on the basis of several isolated teeth from the Late Triassic (Carnian) Tiki Formation, south Rewa Gondwana Basin, Madhya Pradesh, India. The new taxon, characterized by mediolaterally compressed tricuspid and tetracuspid postcanines with incipient root division, is similar to dromatheriids from the Late Triassic of Europe and North America. It also bears some plesiomorphic resemblance to *Therioherpeton* of Brazil. The new taxon further extends the geographic range of the already widespread distribution of dromatheriids and putatively related taxa. It corroborates the hypothesis on the cosmopolitan nature of the Late Triassic terrestrial vertebrate faunas worldwide. Because of the limited known materials and plesiomorphic features, the phylogenetic relationships of dromatheriids to mammals remain uncertain.

KEY WORDS: Dromatheriidae, Cynodontia, Tiki Formation, Late Triassic, India

## INTRODUCTION

Dromatheriids are small to medium-sized carnivores of Late Triassic age. This group of non-mammalian cynodonts ("mammal-like reptiles") were previously reported from North America (Emmons, 1857; Sues et al., 1994; Sues, 2001), central and western Europe (Hahn et al., 1984, 1994; Godefroit, 1997; Godefroit and Battail, 1997; Godefroit et al., 1998). *Therioherpeton*, a cynodont considered by some to be closely related to dromatheriids (Battail, 1991), is known from Brazil (Bonaparte and Barberena, 1975, 2001).

Although first thought to be mammals in the 19<sup>th</sup> century (Emmons, 1857; Osborn, 1886), dromatheriids have been considered non-mammalian cynodonts since the 1920s (Simpson, 1926; Battail, 1991; Hahn et al., 1994; Sues, 2001). Sues (2001) reviewed the latest evidence and concluded that the "mammal-like" features of dromatheriids are shared by many non-mammalian cynodonts, and that dromatheriids are best regarded to be advanced non-mammalian cynodonts, rather than mammals. Because dromatheriids are represented as yet only by very incomplete fossils, there has not been a parsimony analysis of their relationships to other advanced cynodonts. Several workers placed dromatheriids in the Chiniquodontoida (Carroll, 1987; Sigogneau-Russell and Hahn, 1994). Within this grouping, Battail (1991) suggested that dromatheriids are the sister-taxon to *Therioherpeton*. However, the currently available evidence, primarily from isolated teeth, is insufficient for assessing these problems (Sues, 2001). Certainly dromatheriids are

no more closely related to mammaliaforms than are tritheledontids (Battail, 1991; Bonaparte and Barberena, 2001), or possibly more distant from mammals than both tritheledontids and tritylodontids (Luo et al., 2002).

The composition of the family Dromatheriidae is also uncertain. The species of the type genus *Dromatherium* is from North America (Emmons, 1857; Simpson, 1926). The best represented taxon of this group is *Microconodon tenuirostris* (including "*Dromatherium tenuirostris*" of Emmons, 1857), as recently described in detail by Sues (2001). *Pseudotriciconodon wilki* and *Tricuspes* from continental Europe have been placed in the Dromatheriidae (Hahn et al., 1984, 1994; Godefroit and Battail, 1997). However, the assignment of other taxa is questionable. Hahn et al. (1984) included in the Dromatheriidae *Therioherpeton* from Brazil (Bonaparte and Barberena, 1975); but this taxon was subsequently re-assigned by Kemp (1982) to tritheledontids. Battail (1991) also removed *Therioherpeton* from Dromatheriidae, but made it the sister-taxon to Dromatheriidae. Most recently, Bonaparte and Barberena (2001) considered *Therioherpeton* to be the sister-taxon to the clade comprising tritheledontids and mammaliaforms. Hahn et al. (1994; see also Godefroit and Battail, 1997) also assigned *Meurthodon* to Dromatheriidae. Shapiro and Jenkins (2001) noted that *Meurthodon* is too different in its fully divided roots from other dromatheriids and argued that it should not be placed in the Dromatheriidae. Lucas and Oakes (1988) erected "*Pseudotriciconodon chatterjeei* on

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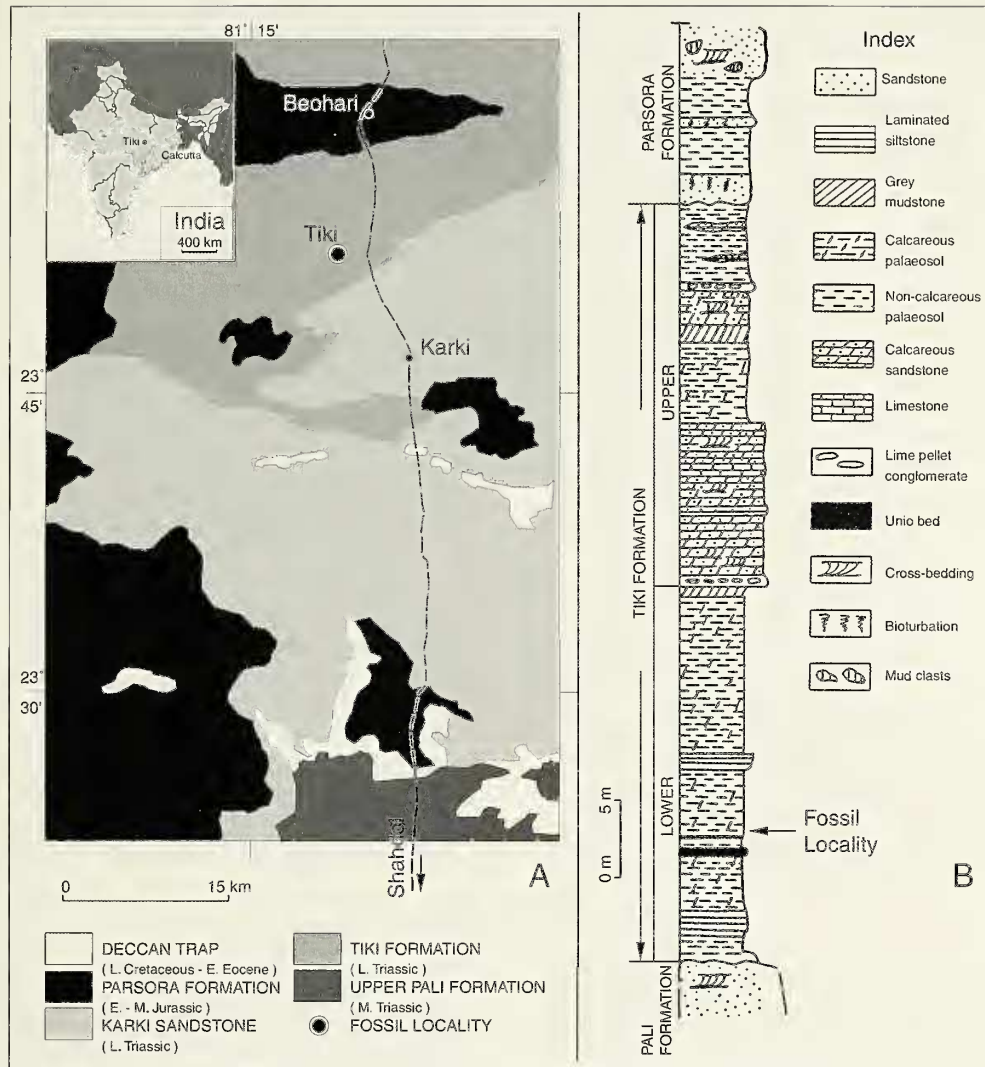


Fig. 1.—A. Simplified geological map of the fossil locality near the Tiki village, Madhya Pradesh State, India. B. The lithostratigraphic section of the Tiki fossil locality (Tiki Formation, the Gondwana Supergroup).

the basis of a specimen from the Upper Triassic of New Mexico, but the assignment of this specimen to *Pseudotriconodon* has been recently questioned (Sues, 2001). In this study, we assume the most conservative

membership for dromatheriids: *Dromatherium*, *Microconodon*, *Pseudotriconodon wildi*, *Tricuspes* and the new taxon from the Upper Triassic (Carnian) Tiki Formation of India to be described below.

### STRATIGRAPHY

The dromatheriid and other non-mammalian cynodont material reported here was collected during the field work of 1997–98 and 1998–99 from an exposure of the calcareous, red mudstones of the Tiki Formation four km southwest of Tiki village in the south Rewa Gondwana Basin, Madhya Pradesh State, India (Fig. 1A). The Tiki formation in the south Rewa Gondwana Basin comprises red mudstone with greenish-gray mottling, calcareous sandstone, cross-bedded feldspathic sandstone and a few lime pellet conglomerate horizons (Fig. 1B).

The Tiki Formation is a part of the Upper Gondwana Group. In the south Rewa Basin it is underlain by the Pali Formation with a local erosional contact. Floral assemblage in the upper part of Pali Formation indicates an Early to Middle Triassic age (Tarafder et al., 1993). The Tiki Formation is unconformably overlain by the Parsora Formation, the lower part of which comprises mudstone of pink, red and lavender colors, brownish ferruginous silty shale and interbeds of sandstone containing clay clasts of varying sizes. The palynomorph evidence



suggests a Rhaetic to Liassic age for the Parsora Formation (Roy Chowdhury et al., 1975; Tarafder et al., 1993).

The Tiki Formation is rich in fossil vertebrates and palynomorphs, which helped to establish its biostratigraphic correlation. The vertebrate assemblage of the Tiki Formation includes: the temnospondyl *Metoposaurus maleriensis* (Sengupta, 1992), the phytosaur *Parasuchus hislopi* (Chatterjee, 1978), the rauisuchid *Tikisuchus romeri* (Chatterjee and Majumdar, 1987) and the rhynchosaur *Hyperodapedon luxleyi* (Benton, 1983). Recently, a primitive morganucodontid mammal *Gondwanadon tapani*, represented by a molar, was discovered from the lower part of the Tiki Formation (Datta and Das, 1996). This vertebrate assemblage, except for the mammalian fossil, is virtually identical to the assemblage of the Maleri Formation of the Pranhita–Godavari valley in the Andhya Pradesh State, another well-known vertebrate-bearing horizon in the Triassic of India.

For intercontinental correlation, the fauna and flora of Tiki Formation can be correlated with the vertebrate fauna of Camp Springs member of the Dockum Formation (Hunt and Lucas, 1991a, b; Chatterjee, 1986; Kutty and Sengupta, 1989), also termed the “North American Land Vertebrate Faunachron A” (Lucas and Hunt, 1993) or Otischalkian (Lucas, 1998). Palynomorphs from the Tiki Formation are closely comparable to the Onslow palynoflora of northwestern Australia (Maheshwari and Kumaran, 1979). This stratigraphically informative

palynomorph assemblage from the Tiki Formation consists of *Aulisporites artimosus*, *Camosporites secatus*, *Duplicisporites granulatus*, *Granuloperculatipoliis* sp., *Enzonalaspories densus*, *E. ignacii* and *E. vigenus*. This palynofloral composition is similar to that of the upper part of the *Samaropollenites speciosus* Zone of the Onslow palynoflora in Australia. The latter has been dated as Carnian (Maheshwari and Kumaran, 1979). The megafloora of the Late Triassic of Indian Peninsula is not sufficiently known for intercontinental correlation (Anderson and Anderson, 1993).

Therefore the Tiki Formation, based on its faunal and floral assemblage, can be compared with the Maleri Formation in the Pranhita–Godavari valley of India and the Carnian faunal assemblages in other non-marine strata elsewhere (Lucas, 1998). Lucas (1998) correlated the Maleri Formation to lower Carnian (Otischalkian of Lucas, 1998). Benton (1994) correlated the Tiki and Maleri Formations to the upper Carnian (Tuvanian), which he considered to be equivalent to the Schilfsandstein–Gipskeuper zonation of the German Keuper. Currently there are no magnetostratigraphic data for correlating the Tiki and Maleri Formations directly to the standard marine sequence.

Abbreviations: GSI, Geological Survey of India; Pal/CHQ, Palaeontological collections (“chiquodontoids”) of GSI in Calcutta. Cusps on postcanines are designated by letters A/a through E/e, following the alphabetical scheme by Crompton (1971, 1974).

## MATERIALS AND METHODS

About 5 metric tons of matrix were collected from the calcareous, red mudstone beds of the Tiki Formation for screen washing. The clay was gradually removed by washing in water. The residue was screened, dried, and manually sorted under a microscope. This procedure has yielded a large number of isolated teeth of ornithischian dinosaurs, phytosaurs, sphenodontians and some cynodonts. Nine teeth that can be referred to dromatheriids have been recovered. Of the nine, eight postcanines described here are considered to belong to a single taxon, whereas the remaining one is distinctly different.

The determination of the relative position of a tooth in the postcanine row is by comparison to the better fossils of *Microconodon* (Sues, 2001). For orientation of the isolated cynodont postcanines, we follow the criteria used by many previous workers, as summarized by Godefroit and Batail (1997). The more convex side is conventionally and arbitrarily regarded as the labial side for both upper and lower postcanines. As the cusp inclination is always distal, if present, the direction of cusp inclination is regarded as distal.

If a contact wear facet is developed, it develops on the labial side of the lower postcanines and on the lingual side of the uppers. Dental contact wear can only develop if the dental replacement rate is sufficiently slow and the upper and lower postcanines have one-to-one opposition (Luo, 1994). These features are absent in most non-mammalian cynodonts, except for such derived taxa as the Gomphodontia (Crompton, 1972), tritheledontids (Gow, 1980) and tritylodontids (Sues, 1986). More common for the carnivorous non-mammalian cynodonts are apical abrasion of cusps. Because the lower teeth always occlude on the lingual side of the upper, the apical abrasions tend to spread from the apex and its associated crest to the occlusal (“contact”) side of the cusp. The apical abrasion of cusps on a tooth is consistently slanted toward the occlusal side of the tooth: the labial side for the lower and the lingual side for the upper. Presence of these wear and abrasion patterns can be utilized for orienting some of the isolated teeth in this sample, for the purpose of description. The orientation of isolated carnivorous cynodont teeth needs to be verified by comparison to the *in situ* teeth in the jaws when better preserved fossils become available.

## SYSTEMATIC PALEONTOLOGY

Clade Cynodontia Owen, 1861  
Family Dromatheriidae Gill, 1872  
Genus *Rewaconodon* **gen. nov.**

*Etymology*.—The genus is named after the Rewa Gondwana Basin of the Madhya Pradesh State, India.

*Diagnosis*.—Postcanine teeth characterized by labio-lingually compressed triconodont-like crown with three to

four cusps aligned in a longitudinal row; incipient division of the root(s) by shallow grooves or depressions on both the lingual and the labial sides of the root(s) and two portions of the root are connected by a thin sheet of dentine. Apical abrasion is developed on at least some cusps on all of the postcanines. Fewer teeth also have occlusal wear between the main cusp and the two

Table 1.—Measurements of postcanine teeth of *Rewaconodon tikiensis* (*Dromatheriidae*, *Cynodontia*) from the Late Triassic (Carnian) Tiki Formation of south Rewa Gondwana basin, Madhya Pradesh, India.

|                         | GSI<br>Pal/CHQ001 | GSI<br>Pal/CHQ002 | GSI<br>Pal/CHQ003 | GSI<br>Pal/CHQ004 | GSI<br>Pal/CHQ005 | GSI<br>Pal/CHQ006 | GSI<br>Pal/CHQ007 | GSI<br>Pal/CHQ008       |
|-------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------------|
| Number of cusps         | 3                 | 3                 | 3                 | 3                 | 4                 | 4                 | 4                 | 4 + cingulid<br>cusps f |
| Main cusp a height (mm) | 1.03              | 0.78              | 0.80              | 0.50              | 1.18              | Not available     | 0.88              | 0.80                    |
| Cusp c height (mm)      | 0.30              | 0.28              | 0.50              | 0.38              | 0.65              | 0.55              | 0.35              | 0.60                    |
| Cusp b height (mm)      | Not available     | 0.15              | 0.35              | 0.35              | 0.55              | 0.33              | 0.28              | 0.30                    |
| Cusp d height (mm)      | —                 | —                 | —                 | —                 | 0.25              | 0.23              | 0.13              | Not available           |
| Tooth length (mm)       | 0.93              | 0.90              | 0.80              | 0.85              | 1.20              | 1.13              | 0.85              | 1.13                    |
| Tooth width (mm)        | 0.42              | 0.31              | 0.38              | 0.31              | 0.27              | 0.44              | 0.22              | 0.29                    |

accessory cusps of the crown. There is no bulging cingulum near the base of the crown, or a constriction at the crown–root junction. *Rewaconodon* differs from the morganucodontid *Gondwanadon* from the same site in having much smaller cusps c and d. *Rewaconodon* differs from chiniquodontids and probainognathians in that the primary cusp of its postcanines is not as recurved distally as in the latter groups. It differs from thrinaxodontids, chiniquodontids and probainognathians in having a more conspicuous (but still incomplete) division of the postcanine roots (Romer, 1969a, b; 1970; Hopson and Kitching, 2001; Abdala, 2000; Abdala and Giannini, 2002). It differs from *Meurthodon* and *Mitrodon* in lacking the complete root divisions in the tetracuspoid postcanines and in being much smaller in size (Sigogneau-Russell and Hahn, 1994; Shapiro and Jenkins, 2001); differs from the multi-cuspoid, and multi-rowed postcanines of diademodontids, traversodontids, and tritylodontids (Crompton, 1972; Sues, 1986); differs from thrinaxodontids, *Prozostrodon* and tritheledontids in lacking the well-developed cingulids; differs from tritheledontids and *Riogradia* in having fewer cusps on the lower postcanines (Bonaparte and Barberena, 2001; Bonaparte et al., 2001). Among all non-mammalian cynodonts, *Rewaconodon* is most similar to *Therioherpeton* and the dromatheriids *Tricuspes* and *Microconodon*. Yet *Rewaconodon* is much smaller (Table 1). Its postcanines are 50% of those of *Therioherpeton*, 50–60% of those of the European dromatheriid *Tricuspes* and *Pseudotriconodon* (Godefroit and Battail, 1997), 70–80% of the teeth of North American dromatheriid *Microconodon*, with exception of one juvenile specimen, as reported by Sues (2001).

*Rewaconodon* differs from *Therioherpeton* and *Microconodon* in that the individual cusps are more stout (less compressed) in cross-section (Bonaparte and Barberena, 1975; Sues et al., 1994); differs from *Tricuspes* in lacking a constricted waist on the mesial aspect of cusp b and the distal aspect of cusp c (Hahn et al. 1994); differs from *Pseudotriconodon* in that the root division is either confined to the tip of the root, or more often completely missing in *Pseudotriconodon*; differs from *Charruodon*, a South American therioherpetid, and *Lepagia*, a Europe-

an cynodont of uncertain affinities, in lacking the shallow constriction between the crown and root found in the latter taxa (Sigogneau-Russell and Hahn, 1994; Abdala and Ribeiro, 2000).

#### *Rewaconodon tikiensis* gen. et sp. nov.

*Etymology*.—The species is named after the village Tiki in the Shadol district, Madhya Pradesh, India (Geological Survey of India topo map No. 64 E) (Figure 1A).

*Holotype*.—GSI Type No. Pal/CHQ-005 (Figure 2), a tetracuspoid lower postcanine tooth, in the collection of the Curatorial Division, Geological Survey of India, Calcutta, India.

*Referred specimens*.—GSI Type Nos. Pal/CHQ-001, Pal/CHQ-002, Pal/CHQ-003, Pal/CHQ-004, Pal/CHQ-006, Pal/CHQ-007 and Pal/CHQ-008. For measurements of these teeth see Table 1.

*Diagnosis*.—As for the genus.

*Type Locality and Type Stratum*.—Lower part of Tiki Formation of the Gondwana Supergroup (Figure 1B); Late Triassic (Carnian); 4 km southwest of the Tiki village (Latitude 23°55'N; Longitude 81°22'E), south Rewa Gondwana Basin, Madhya Pradesh State, India.

#### DESCRIPTION

Four tricuspid postcanines (GSI-Pal/CHQ-001 through Pal/CHQ-004) are interpreted as anterior postcanines, by comparison to those of *Microconodon* (Sues, 2001). Pal/CHQ-001 (Figure 3) is a “premolariform” positioned in the anterior part of the postcanine row. Following the criteria of Godefroit and Battail (1997), we tentatively interpret it as an upper right anterior postcanine. Its principal cusp A has a longer mesial crest than the distal crest. The small and more distal cusp C is raised beyond the crown–root junction. The mesial accessory cusp (B?) is much smaller and lower than the distal cusp C. The crown enamel is smooth; some distinctive, vertical wrinkles are present on both the lingual and labial sides near the base of the main cusp. Main cusp A and distal cusp C show apical abrasion.

One tricuspid tooth (Pal/CHQ-002; Figure 4) is considered to be a lower right anterior postcanine. Main



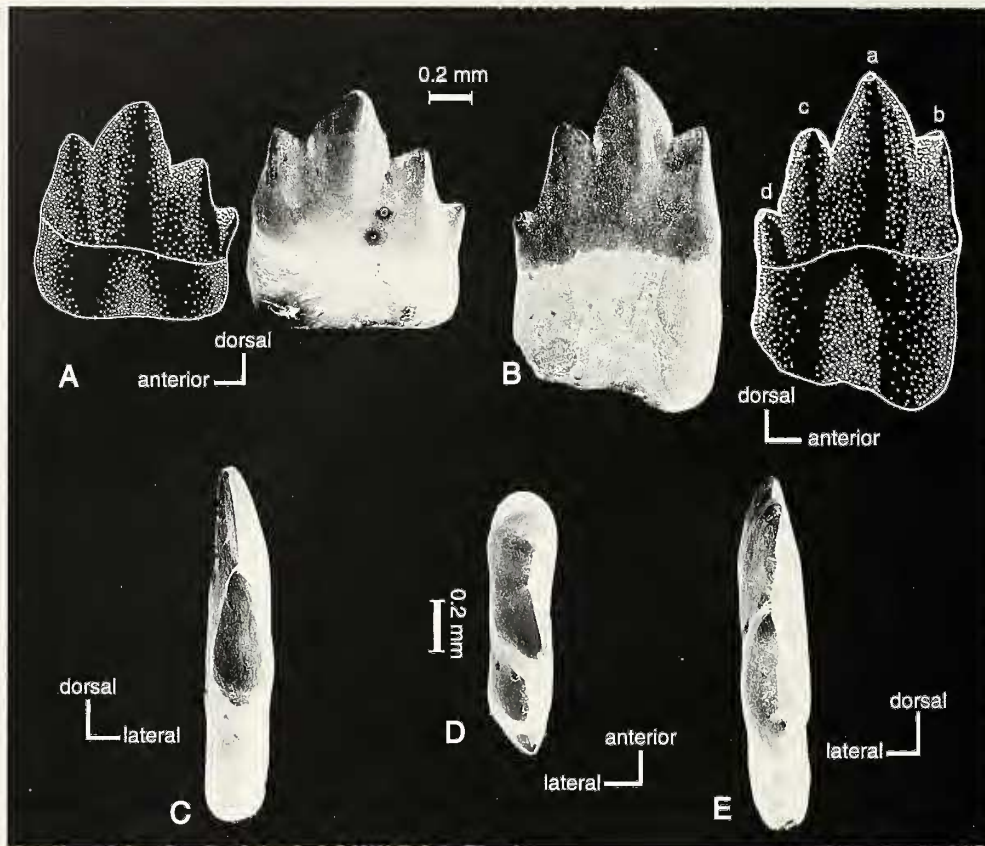


Fig. 2.—Holotype of *Rewaconodon nkiensis* (GSI Pal/CHQ-005: Dromatheriidae, Cynodontia). SEM photographs of a lower left posterior tetracuspoid postcanine: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, dorsal (occlusal) view. E, posterior (distal) view. Cusp designation following Crompton (1974).

cusps a and b are the largest cusps. Its mesial crest is slightly more convex than the distal crest. Accessory cusps b and c are arranged almost symmetrically relative to cusps a and b. There is no cingulid at the base of the crown or constriction at the crown-root junction. The root is incipiently divided by a furrow on both lingual and labial sides; the two portions of the root are connected by dentine such that in the horizontal section the root forms a figure 8. A tricuspid tooth (Pal/CHQ-003: Figure 5) is an upper right postcanine. This tooth differs from other tricuspid teeth in having much larger mesial and distal accessory cusps. The crown of Pal/CHQ-004 (Figure 6) is symmetrical labiolingually and has a similar curvature on both sides; its crown is extensively damaged. Thus its orientation is uncertain.

The four tetracuspoid teeth (GSI-Pal/CHQ-005 to 008) are considered to be the posterior postcanines by comparison to those of *Microconodon* (Sues, 2001), *Therioherpeton* (Bonaparte and Barberena, 1975, 2001) and, to a lesser extent, to *Mitrodon* (Shapiro and Jenkins, 2001). The holotype specimen (GSI-Pal/CHQ-005: Figure 2) is a posterior lower postcanine from the left side, following the morphological criteria of orienting the

isolated cynodont postcanine teeth by Godefroit and Battail (1997). Primary cusp a is labiolingually compressed and slightly recurved, with mesial and distal crests extending from the apex. Mesial cusp b has a rounded mesial face, and a distal crest extending from the apex. Distal cusp c is lower than mesial cusp b. The distal cuspule d is the smallest of the four cusps. Two wear facets are present on the labial side of the crown, one in the valley between cusps b and a and the other between cusps a and c. The enamel surface near the crown and root junction slightly bulges, but there is no distinctive cingulid or constriction to separate the enamel surface of the crown from the dentine surface of the root.

Two tetracuspoid teeth (Pal/CHQ-007, 008: Figure 7) are also likely to be left lower posterior postcanines, but both show a more mesio-distal asymmetry than the holotype specimen. Principal cusp a of both teeth is the largest cusp. Its mesial crest is much longer than the distal crest, making the cusp appear slightly recurved. Distal cusp c is only slightly lower than and in close proximity to cusp a. Mesial cusp b is much smaller than d. Distal cusp d is variable: well developed in the type specimen (Pal/CHQ-005), but small in one specimen (Pal/CHQ-007),

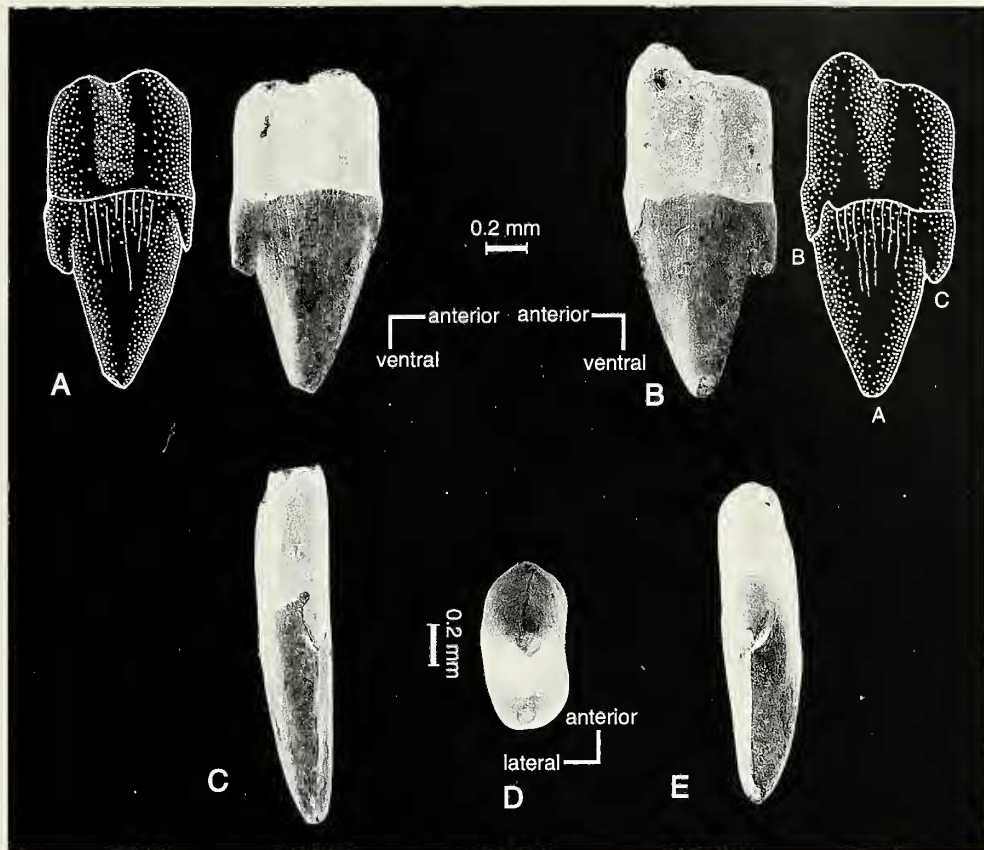


Fig. 3.—*Rewaconodon tikiensis* (GSI Pal/CHQ-001: Dromatheriidae, Cynodontia). An upper, premolariform (anterior) postcanine from right side: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, crown (occlusal) view. E, posterior (distal) view.

and vestigial in the other (Pal/CHQ-008). Another variable feature is anterolabial cingulid cuspule f (after alphabetical designation of Crompton, 1974), only present in Pal/CHQ-008 but absent in other tetracuspoid teeth. All tetracuspoid teeth have developed some degree of apical abrasion at the tips of the tooth cusps.

We tentatively interpret Pal/CHQ-006 (Figure 8) as a lower right postcanine near the middle of the tooth row because it is much wider and slightly shorter than other tetracuspoid teeth, fitting the profile of the "middle" postcanines in tooth row of some advanced cynodonts (Osborn and Crompton, 1971). Pal/CHQ-006 has much smaller cusps b and c than other tetracuspoid teeth. Cusp b is positioned at the mesial end of the tooth near the cingulid level, and is less distinctive than the same cusp in other tetracuspoid teeth.

#### DISCUSSION

*Taxonomy.*—The morphological and size differences of *Rewaconodon* from other dromatheriids and the wide geographic separation of the Tiki locality from the localities in North America and Continental Europe make it reasonable for us to recognize *Rewaconodon tikiensis*

gen. et sp. nov. as a new taxon of the Dromatheriidae. All the specimens come from the same locality of the Tiki Formation, and have a relatively narrow range of variation in crown and root structure. The morphological variation among the teeth can be attributed to different positions in the tooth-row. Therefore we assign these teeth to a single taxon *R. tikiensis*. More detailed taxonomic justifications are given below.

The postcanines of *Rewaconodon* have a suite of primitive dental characters of advanced non-mammalian cynodonts. Among the known non-mammalian cynodont groups of the Late Triassic, *Rewaconodon* are most similar to *Microconodon* of North America (Simpson, 1926; Sues, 2001) and *Tricuspes* of Europe (Hahn et al. 1994; Godefroit and Battail, 1997), and to a lesser extent to *Pseudotriconodon* of Europe (Hahn et al., 1984, 1987; Sigogneau-Russell and Hahn, 1994). Nonetheless, *Rewaconodon* can be unambiguously distinguished from all other taxa hitherto placed in the Dromatheriidae (Hahn et al., 1994: fig.2). It differs from *Microconodon*, *Dromatherium*, and *Lepagia* in having vertical wrinkles (striations) on the enamel near the base of the principal cusps of the tricuspid teeth, and in having smaller teeth (see "diagnosis" and Table 1).



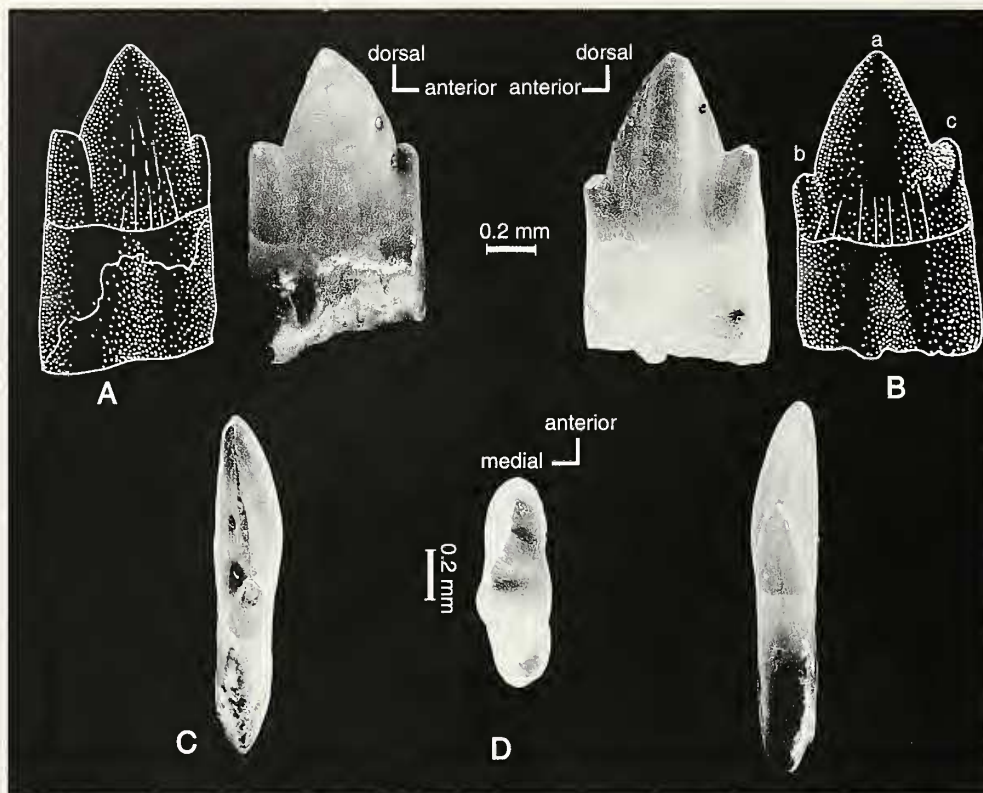


Fig. 4.—*Rewaconodon tikiensis* (GSI Pal/CHQ-002: Dromatheriidae, Cynodontia). Lower right anterior postcanine: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, crown (occlusal) view. E, posterior (distal) view.

All eight cynodont teeth collected from the Tiki sites have essentially a "triconodont-like" design, with three or four labiolingually compressed cusps in a straight alignment. This sample also shows a relatively narrow range of size variation. The length of the crown ranges from 0.80 mm to 0.93 mm for the tricuspoid teeth, and 0.85 mm to 1.20 mm for the tetracuspoid teeth. The height of the crown varies from 0.50 mm to 1.03 mm for the tricuspoid teeth, from 0.70 mm to 1.18 mm for the tetracuspoid teeth (Table 1). These teeth of *Rewaconodon tikiensis* are smaller than those currently known in *Microconodon* and other dromatheriids.

The morphological variation of the tricuspoid and tetracuspoid postcanines corresponds, in some degree, to the gradient variation along the postcanine series, as commonly seen in many (but not all) advanced non-mammalian cynodonts (e.g., Osborn and Crompton, 1971). *Microconodon* shows an increase in cusp number and more equal size of cusps in the more posterior teeth (Sues, 2001). It is likely that more than one generation of replacement teeth are represented in this sample; so some of the morphological variation may be related to the differences between successive generations of teeth at the same tooth locus.

For practical purposes of separating the taxa of this family from other advanced non-mammalian cynodonts,

there is a combination of plesiomorphic tooth crown features of the postcanines, such as the absence of basal constriction at the crown-tooth junction. Current evidence for supporting the monophyly of this family is quite limited; therefore the validity of the Dromatheriidae must be tested when better fossils become available in the future. However, the limited dental characteristics are not sufficient for resolving the complex relationships of dromatheriids to chiniquodontids, to *Meurthodon* and *Mitrodon*, and to *Riograndia*, *Therioherpeton*, and probainognathians, as already noted by several recent studies (Bonaparte and Barberena, 2001; Shapiro and Jenkins, 2001; Sues, 2001).

*Dental morphology.*—The wear patterns are highly variable among postcanines in this sample assigned to *Rewaconodon*. Six of the postcanines assigned show some degrees of apical abrasion, a primitive pattern of the carnivorous non-mammalian cynodonts. Irregular apical abrasion may be associated with more frequent dental replacements than the diphyodont dental replacement as the teeth with less frequent replacement tend to have precise match of the crown but less irregular abrasion. The presence of apical abrasion does not mean that the upper and lower postcanines have a one-to-one occlusal contact. Several postcanines show that the apical abrasion of a late stage can spread from apices to the occlusal

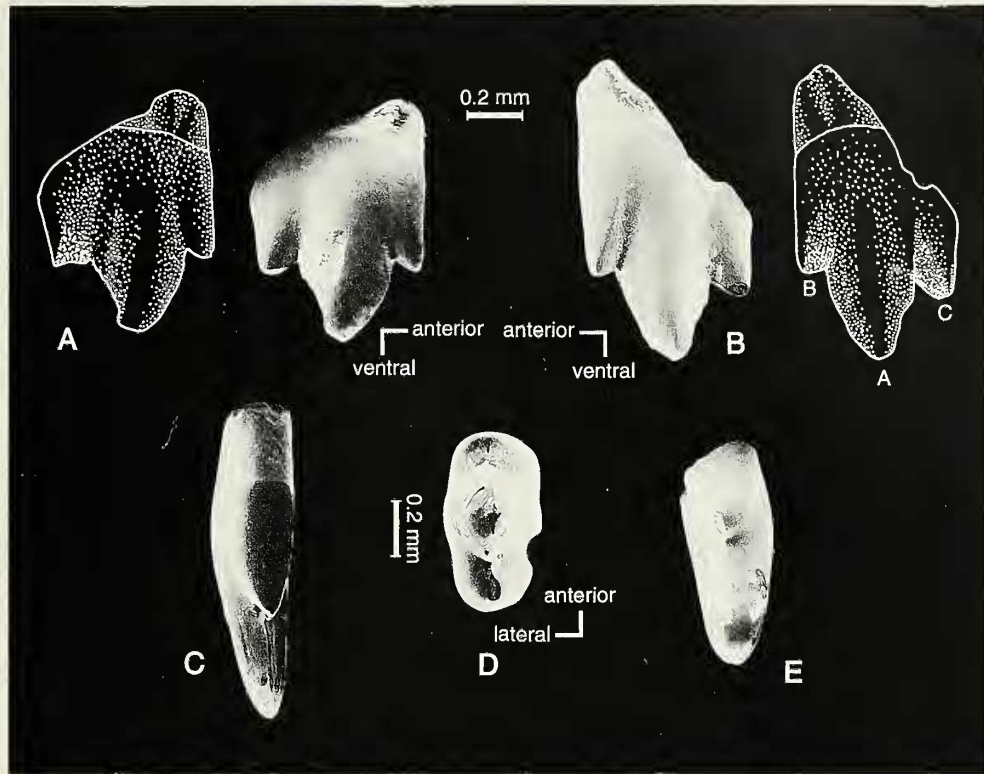


Fig. 5.—*Rewaconodon tikiensis* (GSI Pal/CHQ-003; Dromatheriidae, Cynodontia). Upper right anterior postcanine: A, lateral (labial) view. B, medial (lingual) view. C, anterior (mesial) view. D, crown (occlusal) view. E, posterior (distal) view.

contact surfaces on the cusps (e.g., Pal/CHQ-003, Pal/CHQ-004, Pal/CHQ-007, Pal/CHQ-008; Figures 5, 7 and 8).

Two teeth of *Rewaconodon* show some limited development of occlusal wear in the valleys between the principal cusp a and mesial cusp b (Pal/CHQ-003, Pal/CHQ-005). This wear is similar to the early-stage wear facets of morganucodontans and kuehneotheriids, the two most primitive groups of mammaliaforms in which the wear-facets have constant topographic relations to the cusps (Mills, 1971, 1984; Crompton 1974). Development of constant wear facets requires that the upper and lower postcanines have a one-to-one correspondence. If wear facets are present, it would also suggest that the individual teeth had a longer functional life, which may in turn indicate slower tooth replacement (Luo, 1994). In several Rhaeto-Liassic mammaliaforms, the beveled facets develop after a substantial amount of enamel surface was removed by the initial wear (Crompton, 1974; Crompton and Jenkins, 1979; Crompton and Luo, 1993). In the current sample of teeth referred to *Rewaconodon*, this type of well-matched and beveled facets has not been observed. It should be noted that the derived occlusal wear facets (e.g., on Pal/CHQ-005) are not as common as the plesiomorphic apical abrasion that is present in all of the teeth assigned to *Rewaconodon*. The indirect evidence so far suggests that *Rewaconodon* probably lacked the

one-to-one opposition of the upper and lower teeth required for the extensive development of dental wear facets.

Wear facets can occur on the postcanines of derived carnivorous cynodonts, but their presence is not a consistent feature among these cynodonts. So far, only the tritheledontid *Pachygenelus* is known to have developed the wear facets on the postcanines, although wear facets were developed across several cusps and lack consistent correspondence to individual cusps as in mammals (Gow, 1980). In the more derived mammaliaform *Sinoconodon*, a limited amount of wear is present on some posterior molars, but these molars lack consistent correspondence to individual cusps due to the lack of one-to-one correspondence of the upper and the lower molars and possible replacements of the molariform postcanines (Crompton and Luo, 1993; Zhang et al., 1998). Development of apical abrasion is most likely a primitive feature among the advanced non-mammalian cynodonts and mammaliaforms because it occurs not only in *Rewaconodon*, *Pachygenelus* and morganucodontans, and but also in other derived non-mammalian cynodonts, although less frequently in the more plesiomorphic groups.

Division of the postcanine roots was traditionally viewed as a derived, mammal-like characteristic, as discussed by Kemp (1983; also Rowe, 1988; Wible,



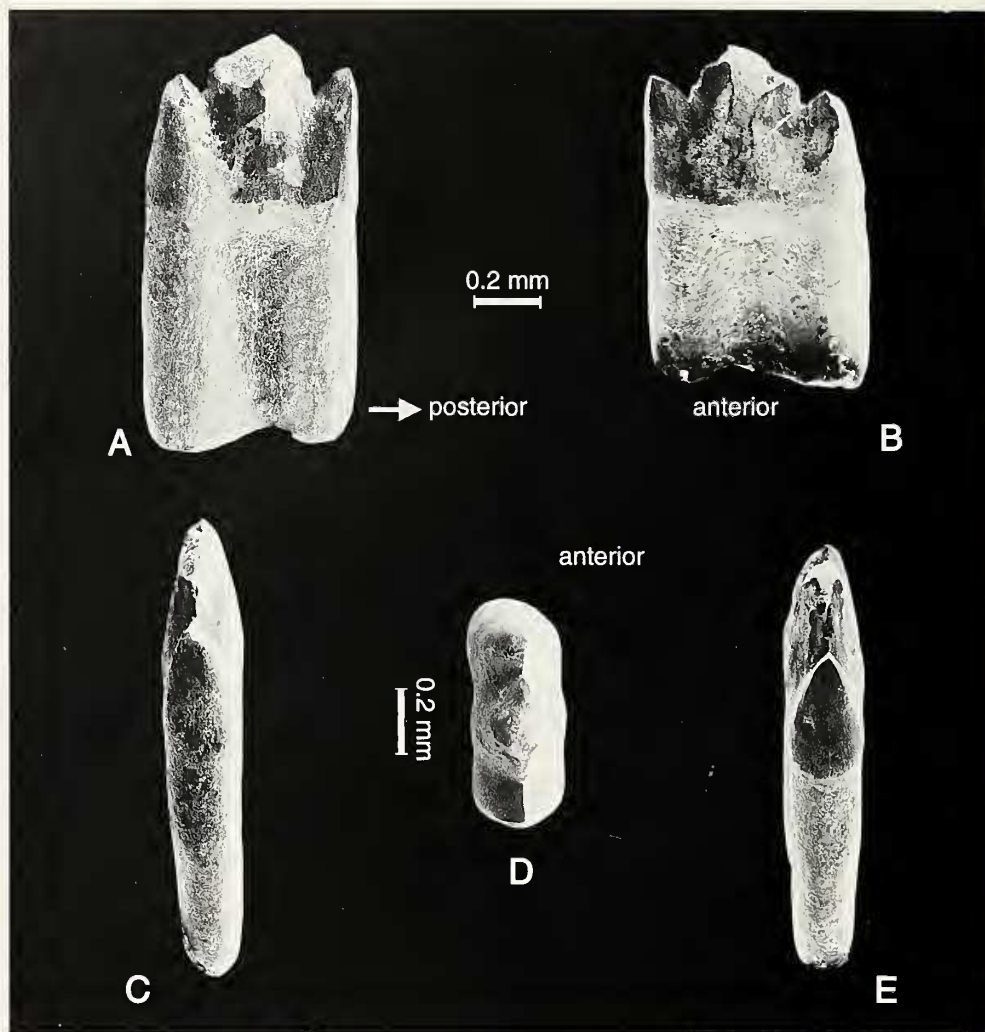


Fig. 6.—*Rewaconodon tikiensis* (GSI Pal/CHQ-004; Dromatheriidae, Cynodontia). Anterior postcanine (orientation uncertain): A, lateral (labial) view. B, medial (lingual) view. C, anterior (?) view. D, crown (occlusal) view. E, posterior (?) view.

1991; Shubin et al., 1991). More recent studies have shown that this feature has a more complex systematic distribution among the groups of advanced cynodonts and early mammaliaforms (e.g., Cui and Sun, 1987; Luo, 1994; Sigogneau-Russell and Hahn, 1994). *Rewaconodon*, *Mitrodon* and *Microconodon*, all of which were recently discovered or restudied, demonstrate that root division and its precursor condition have an even wider systematic distribution than previously thought.

Several cynodonts are known to have a degree of variation of the root division (Luo, 1994; Shapiro and Jenkins, 2001). Incipient division of the root occurs in *Pachygenelus* from North America (Shubin et al., 1991), but it was variable and less developed in the African *Pachygenelus* (Gow, 1980). A derived condition of root division may occur in cynodonts that are otherwise very primitive in crown characters and dental replacement.

Complete root division is present in *Mitrodon*, but this non-mammalian cynodont retains the primitive alternating, multiple and wave-like dental replacement (Shapiro and Jenkins, 2001). Among mammaliaforms, root division of postcanines is variable in different tooth loci in *Sinoconodon* (Luo, 1994), in some molariform teeth of *Kuehneotherium* (Parrington, 1971) and *Morganucodon watsoni* (personal observation). In short, the presence of some degree of root division suggests that dromatheriids (including *Rewaconodon*) are more derived than other cynodonts that lack this feature, such as: thrinaxodontids, probainognathians, chiniquodontids (*sensu stricto*), and gomphodonts (*sensu stricto*). However, presence of root division and its precursor condition, by themselves, are not sufficient to indicate a close mammalian affinity. By the incipient root division, dromatheriids are no more closely related to mammals than either tritylodontids

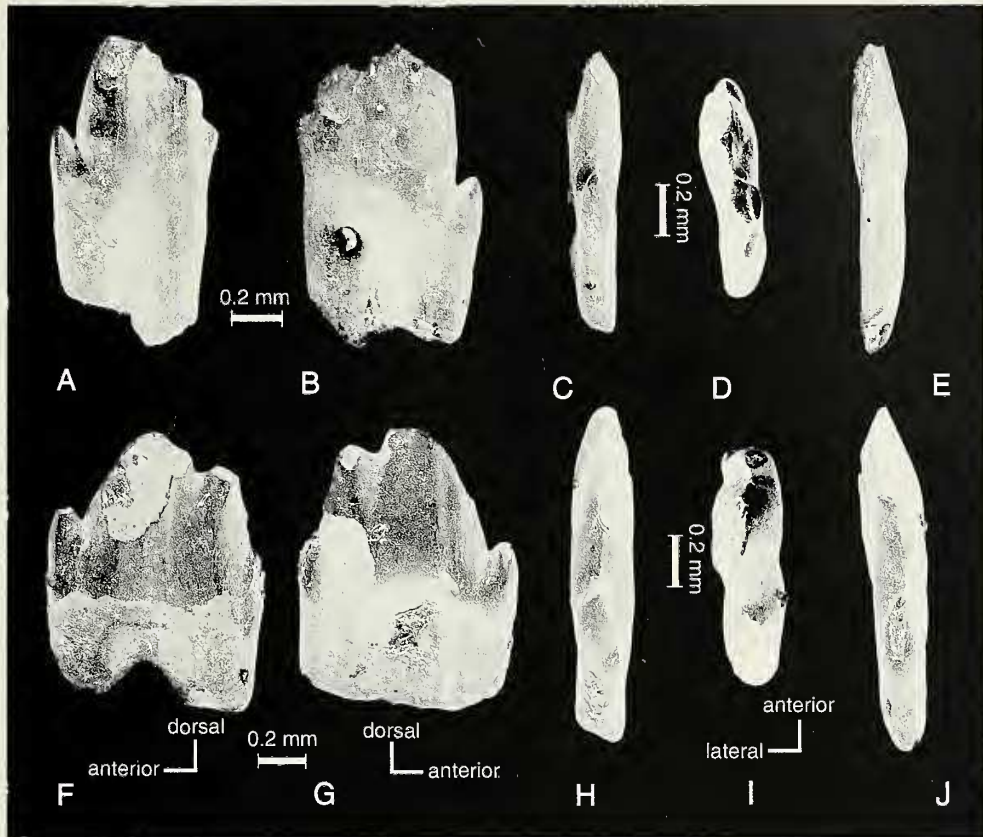


Fig. 7.—*Rewaconodon tikiensis* (Dromatheriidae, Cynodontia); Lower left tetracuspид postcanines. GSI Pal/CHQ-007: A, lateral (labial) view. B, medial (lingual) view. C, posterior (distal) view. D, crown (occlusal) view. E, anterior (mesial) view. GSI Pal/CHQ-008: F, lateral (labial) view. G, medial (lingual) view. H, anterior (mesial) view. I, crown (occlusal) view. J, posterior (distal) view.

(with full division of multiple roots) and tritheledontids (also with incipient division of roots) (Sues, 2001; Luo et al., 2002).

Although many non-mammalian cynodonts have developed some degree of root division, dromatheriids, *Therioherpeton* and *Pachygelemus* are unique in that the dividing grooves extend for the full length of the root on the lingual and labial sides. This is one of the few derived characters useful for distinguishing them from other derived non-mammalian cynodonts. The postcanine root structure is nearly identical in *Rewaconodon*, *Dromatherium*, *Microconodon* and *Therioherpeton* (Simpson, 1926; Bonaparte and Barberena, 1975, 2001; Sues, 2001). The root structure of the tetracuspид postcanine of *Rewaconodon* is also similar to that of *Lepagia* but different from (better divided than) that of *Pseudotriciconodon* (Hahn et al., 1984).

**Biogeographic implications.**—The newly discovered dromatheriid *Rewaconodon* also has biogeographic implications. Through the transition from the Late Triassic to Early Jurassic, the global terrestrial tetrapod assemblages are dominated by widely spread and

cosmopolitan families, indicating that there were few geographic barriers to the exchanges of terrestrial tetrapods among major landmasses (Shubin and Sues, 1991). The newly recognized dromatheriid *Rewaconodon* in the Tiki Formation of India extends the geographic distribution of dromatheriids, previously known from the Carnian sediments of the Newark Supergroup and the Dockum Group of North America (Sues et al. 1994; Lucas and Oakes, 1988; Sues et al. 1994), and from Norian-Rhaetian sediments of Europe (Hahn et al. 1994; Godefroit, 1997; Godefroit and Battail, 1997; Godefroit et al., 1998). These dromatheriids are possibly closely related to therioherpetids from the Carnian strata of the Santa Maria Formation of Brazil (Hahn et al., 1987, 1994; Battail, 1991; Bonaparte and Barberena, 1975, 2001; Abdala and Ribeiro, 2000). This new evidence corroborates the hypothesis that the faunal transition from the Late Triassic to the Early Jurassic is accompanied by an increasingly cosmopolitan nature of the continental tetrapod assemblages (Shubin and Sues, 1991).



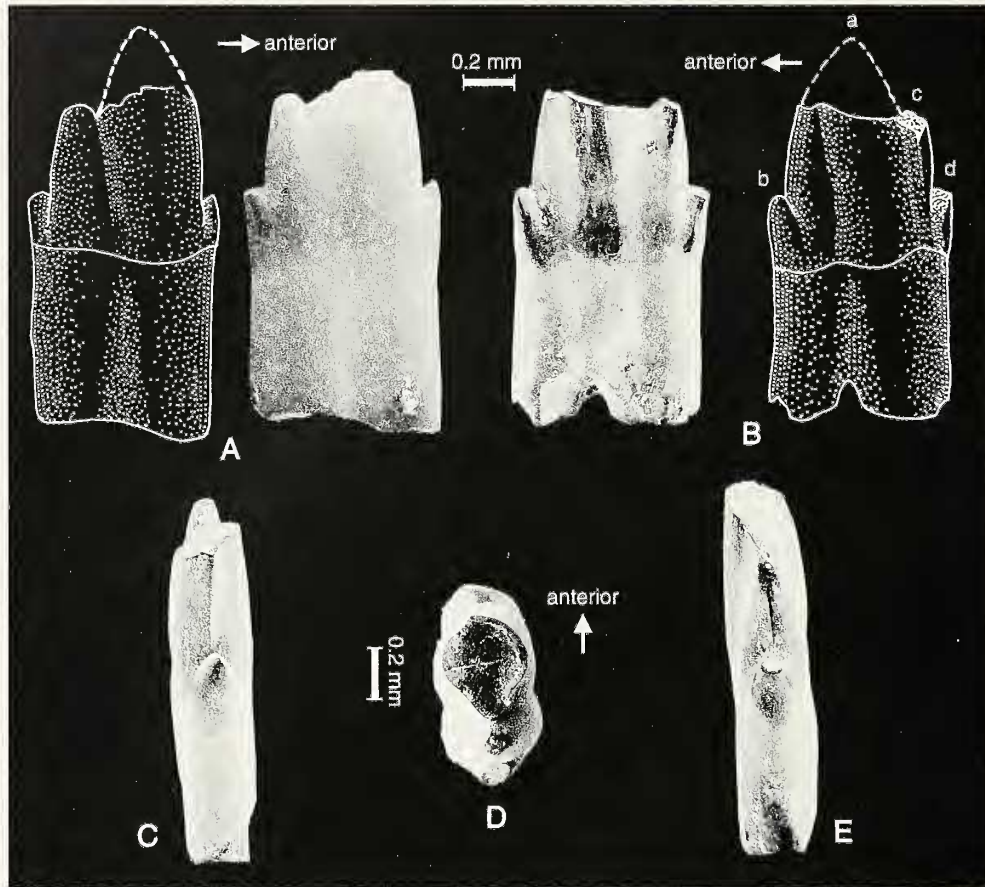


Fig. 8.—*Rewaconodon tikiensis* (GSI Pal/CHQ-006; Dromatheriidae, Cynodontia). A tetracuspid postcanine (tooth locus and orientation uncertain): A, lateral (labial) view. B, medial (lingual) view. C, anterior (?) view. D, crown (occlusal) view. E, posterior (?) view.

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